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ORIGINS AND SUBFAMILIAL RELATIONSHIPS OF *DIPROTODON* (DIPROTODONTIDAE, MARSUPIALIA)

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ABSTRACT

The Pleistocene *Diprotodon* is shown to be similar in dental and cranial anatomy to the Pliocene *Euryzygoma*. Although sufficient characters indicate the generic distinction of the two kinds of diprotodontids, they are not regarded as distinctive enough to warrant subfamilial separation. Accordingly, all forms regarded previously as nototheriines are referred to the Diprotodontinae.

One of the enigmas of marsupial origins is the ancestry of the highly specialized *Diprotodon*. Species of this genus occur in Pleistocene deposits apparently without closely related ancestors in older deposits.

While examining large series of diprotodontid specimens from the late Pliocene Chinchilla Sand, it became apparent that dental variation in the nototheriine *Euryzygoma dunense* incorporated many of the characters otherwise thought to be diagnostic of *Diprotodon*.

Specimen numbers with an F prefix are from the Queensland Museum fossil vertebrate collections. A P prefix indicates a specimen from the palaeontological collections of the South Australian Museum.

DIAGNOSTIC CHARACTERS OF DIPROTODON

Stirton, Woodburne, and Plane (1967) diagnose the Diprotodontinae (which they regard as containing only *Diprotodon*) as follows: P^4 small, quadritubercular, complex, lophodont, with 'horse-hoof' pattern, metacone and paracone distinct, protocone connected to metacone, no hypocone, small parastyle; P_4 bilophodont, lophs uniting with wear to form 'horse-hoof' pattern, paralophid reduced, with posterior cingulum; molars without midlinks, narrow deep transverse median valleys with cement; palate has deep groove between diastemal crests; no epitympanic fenestra in superficies meatus posterior to glenoid fossa; large postglenoid process. In addition, it is often noted (e.g. Marshall 1973) that teeth of *Diprotodon* have a characteristic punctate surface texture.

COMPARISON OF DIPROTODON AND EURYZYGOMA

P^4: F3370 shows the common *Euryzygoma* condition of P^4 with a distinct protocone connected to a wide parametacone by a protoloph. There is a marked swelling on the posterobuccal flank of the protocone, and on the postero-lingual flank of the parametacone. An alternative and less common condition is shown by F3367 where these swellings actually contact, thereby enclosing a central basin. Except for the parametacone, this is very similar to the *Diprotodon* condition and almost identical to one *Diprotodon* specimen (F6635). Although no *Euryzygoma* P^4 observed has a separate paracone and metacone, the parametacone of some (e.g. F7972) is very wide and on its buccal flank a vertical groove suggests demarcation between a paracone and metacone. In any case, although in most unworn specimens of *Diprotodon* the paracone and metacone are distinct, they are frequently very close together, and joined by a high parametacone crest. In slightly worn specimens (e.g. F7971), the metacone and paracone are undifferentiable as the ends of the narrow parametacone crest. In *Eurzygoma*, as in *Diprotodon* a small parastyle is normally present (e.g. F8941) but sometimes is very small (e.g. F7973).

P_4: Comparison of P_4 in *Diprotodon* and *Euryzygoma* is limited because there are no lower premolars of *Euryzygoma* sufficiently unworn to clearly determine the crown pattern. P_4 of the holotype of *E. dunense* (F376) and F5972 give some indication of shape and suggest the tooth is not horse-hoof shaped as it is in some *Diprotodon* (e.g. P10559). In F8943, an isolated P_4 of *Diprotodon*,

there are basically two high transverse crests, the metalophid and hypolophid, which are barely connected by an antero-lingual ridge from the hypolophid. With wear this would produce the normal horse-hoof pattern of *Diprotodon*. The anterior crest or, metalophid is also the posterior wall of a solid triangular trigonid. This pattern is not markedly different from that of *Euryzygoma*. In F5972 there is a low hypolophid and a higher trigonid. The trigonid posterior wall is the metalophid. A small crest extends posteriorly from the lingual end of the metalophid towards the hypolophid, and if not homologous, is at least analogous to the lingual crest linking the meta- and hypolophids of *Diprotodon*. A specimen of *Diprotodon* illustrated by Owen (1877, pl. 124) shows a P_4 in which the linking crest extends postero-lingually from the metalophid as in *Euryzygoma*.

MOLARS: As in *Diprotodon*, the molars of *Euryzygoma* lack midlinks and have narrow, deep transverse median valleys. The molars and premolars normally have a punctate enamel surface made of many fine irregular vertical crenulations. No specimen of *Euryzygoma* has been observed with cement. Although it is not uncommon for specimens of *Diprotodon* (e.g. F6633) to lack cement, this may in part result from older specimens having had their cement removed by preparators.

SKULL: The cranial characters regarded by Stirton, Woodburne and Plane (1967) to diagnose diprotodontines are, as they note, also present in nototheriines. A skull of *Euryzygoma* from the Allingham Formation figured in Archer and Wade (1976) indicates that not all members of this genus had grossly enlarged zygomatic flanges, and such a structurally simple *Euryzygoma* could have been ancestral to *Diprotodon*.

DISCUSSION

Diprotodon is so far only recorded with certainty from Pleistocene deposits (Stirton, Woodburne and Plane 1967). Marshall (1973) lists it in the Fisherman's Cliff local fauna, regarded by him to be either late Pliocene or Pleistocene. This record is based only on a tooth fragment and is doubtful. Woods (1962) records *Diprotodon* from the late Pliocene (Bartholomai 1972) Chinchilla Sand. This record is probably based on one or more of the *Diprotodon*-like P^4 specimens described above. *Euryzygoma* is so far only recorded from the Chinchilla Sand and the older Allingham Formation (Archer and Wade 1976). There is thus no overlap between species of *Diprotodon* and *Euryzygoma*.

Morphological evidence presented above suggests that variation present in *Euryzygoma* foreshadows that of *Diprotodon*. The differences species of *Diprotodon* show from those of *Euryzygoma*, including the much larger size, higher-crowned teeth, distinct P^4 para- and metacones, and details of skull and post-cranial morphology, although clearly indicative of different genera, are probably not indicative of different subfamilies. The view proposed here is that *Euryzygoma* be regarded as structurally ancestral to *Diprotodon*, and that *Diprotodon*, *Euryzygoma*, and all other genera regarded by Stirton, Tedford and Plane (1967) to be nototheriines, be regarded as diprotodontines.

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